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Temperature-dependent development and somatic growth in two allopatric populations of *Acartia clausi* (Copepoda: Calanoida)

Sérgio Miguel Leandro[1,*], Henrique Queiroga[1], Laura Rodríguez-Graña[2], Peter Tiselius[3]

[1]Department of Biology, University of Aveiro, Campus Universitário de Santiago, 3810-193 Aveiro, Portugal
[2]Departamento de Ecología, Facultad de Ciencias, Universidad de la República, Iguá 4225, Montevideo, Uruguay
[3]Göteborg University, Department of Marine Ecology, Kristineberg Marine Research Station, 450 34 Fiskebäckskil, Sweden

ABSTRACT: This study compares the effect of temperature on the post-embryonic development time and weight-specific growth rate in 2 populations of *Acartia clausi* from different biogeographic areas (northern and southern Europe). Development was followed from nauplius I to adult at 3 temperatures (10, 15 and 18°C) at saturating food conditions. The relationship between development time and temperature was established by fitting Belehradek's function. The northern population had a shorter generation time at all temperatures. At 10°C, the development time was estimated to be 33.9 and 36.4 d decreasing to 16.3 and 17.4 d at 18°C for the northern and southern populations, respectively. Prosome length decreased with temperature, and the southern population had longer individuals at all temperatures. ANCOVA revealed a significant ($p < 0.001$) positive effect of temperature on the growth rates, and naupliі grew faster than copepodites (except at 18°C in the southern population and 20°C in the northern population). Significant differences between populations were noted during larval growth, with naupliі from the north growing faster at high temperatures (18°C). The results indicate that the 2 *A. clausi* allopatric populations subjected to different temperature regimes have different temperature responses, in particular at high temperatures.

KEY WORDS: Temperature · Development time · Weight-specific growth rate · *Acartia clausi* · Ria de Aveiro (Portugal) · Gullmarsfjord (Sweden)

INTRODUCTION

Temperature is an important environmental factor for ectotherm organisms like copepods, and it strongly affects vital physiological rates, such as respiration (e.g. Roddie et al. 1984, Gaudy et al. 2000) and excretion (e.g. Gaudy et al. 2000). Along with food conditions, temperature can also modify the life-history traits of copepods through its influence on mortality rates (e.g. Hirst & Kiørboe 2002), egg production (e.g. Halsband-Lenk et al. 2002) and growth and development rates (Campbell et al. 2001, Hirst & Kiørboe 2002).

Calanoid copepods often dominate the zooplankton in terms of abundance and biomass, and some species occur over wide biogeographic regions (Mauchline 1998). The neritic copepod *Acartia clausi* Giesbrecht has been recorded in different areas of the Atlantic Ocean, such as the North Sea (Tiselius et al. 1991), Irish Sea (Castellani & Lucas 2003), English Channel (Lindley et al. 1997), Cantabrian coast (Quevedo et al. 1999) and northwest coast of Portugal (Morgado et al. 2003) as well as in other areas including the Mediterranean Sea (Gaudy et al. 2000), Black Sea (Gubanova et al. 2002), Gulf of Guinea (Pagano et al. 2003) and Pacific Ocean (Gomez-Gutierrez et al. 1999).

*Email: sleandro@bio.ua.pt

The populations are subjected to local conditions, creating site-specific adaptations and eventually genetic differences. Reduced gene flow between populations will over time create different genotypes. The degree of genetic exchange between populations depends on the capacity that a given sub-population has to remain and keep isolated in a given area. *Acartia* spp. species are common in extremely advective regions, such as coastal areas and estuaries, but can establish persistent populations. *A. clausi* is able to maintain isolated populations even at relatively short spatial scales, in contrast to other species such *Calanus* spp. (Bucklin et al. 2000).

The retention of *Acartia* spp. populations in a given region may be attributed to the combined effect of the swimming behaviour that allows regulation of vertical distribution (Kouassi et al. 2001); the production of diapause eggs (Castro-Longoria 2001) in response to unfavourable environmental conditions; and life-history traits such as short generation times and high reproductive potential. The evidence that genetic differences occur among allopatric populations of *A. clausi* implies that population-specific responses to environmental conditions could exist.

The present study was aimed at comparing the effects of temperature on the development and growth rate of 2 populations of *Acartia clausi* from northern (58° 15′ N, 11° 27′ E) and southern Europe (40° 38′ N, 8° 44′ W). The southern population (Ria de Aveiro, Portugal) experiences a temperature range of 11 to 20°C and shows abundance peaks in July and October, when water temperature varies from 17 to 20°C (S. M. Leandro unpubl.). The northern population (Gullmarsfjord, Sweden) lives where the water temperature fluctuates between –1 and 20°C and is most abundant from June to August (14 to 20°C, Eriksson 1973). Our null hypothesis was that development time and growth rates of the 2 populations were not different when reared at the same temperature. To test this, development was followed from nauplius I to adults at 3 temperatures (10, 15 and 18°C) and at saturating food conditions.

MATERIALS AND METHODS

Parental cultures. In order to avoid confounding effects of field temperature on development and growth, all copepods for the parental cultures were collected at nearly the same water temperature (16°C), but at different seasons for the northern and southern populations. Accordingly, *Acartia clausi* were collected in the Gullmarsfjord, Sweden (58° 15′ N, 11° 27′ E, northern population), in summer of 2002 and in Ria de Aveiro, Portugal (40° 38′ N, 08° 43′ W, southern population) in spring 2003. We did not replicate the sampling of parental animals but studied the temperature response within each population, represented by a single subsample. Although genetic differences can occur over short distances (Bucklin et al. 2000), the sampling areas are highly dynamic and the populations continuously reproducing, and we assumed that sampling several thousand females on 1 occasion would give a good representation of the population in the area.

The copepods were caught with horizontal tows at 2 m using a 200 µm mesh net fitted with a 10 l plastic bag as a cod end. After collection, the samples were diluted in surface water and brought to the laboratory within 1 h. In the laboratory, ca. 2000 females of *Acartia clausi* from each location were sorted out using a binocular microscope and transferred to 20 l buckets. The animals were fed with a mixture of the diatom *Thalassiosira weissflogii* (equivalent spherical diameter, ESD = 14.5 µm) and the cryptophyte *Rhodomonas* sp. (ESD = 6.7 µm). The microalgae were grown in f/2 medium (Guillard 1962) at 20°C under a 12 :12 h light:dark cycle. Both algal strains were provided by the Marine Algal Culture Centre at Göteborg University (GUMACC).

Eggs from the field-caught females were harvested daily, rinsed in filtered seawater and stored in 10 ml plastic tubes at 4°C in the dark. Parental stock cultures for the northern and southern populations were subsequently started with the eggs collected from the corresponding field culture and placed in 40 l carboys containing filtered seawater (< 0.2 µm, salinity 32 psu) and maintained at 18°C. The cultures were fed *Rhodomonas* sp. ad libitum during naupliar development and a mixture of *Rhodomonas* sp. and *Thalassiosira weissflogii* after the appearance of copepodites.

Growth experiments. Growth experiments started after the parental cultures were acclimated for 1 generation (Table 1). For each treatment/replicate ~10 000 eggs were harvested from the corresponding stock and

Table 1. *Acartia clausi*. Experiments performed. Ambient temperature, date of collection of the field populations, end of acclimation period and dates for each experiment. Eggs for experiments were stored at 4°C in the dark from end of acclimation to start of experiments

	Northern	Southern
Ambient temperature (°C)	16.8	15.6
Date of collection	19 Jul 2002	24 Feb 2003
End of acclimation	20 Aug 2002	25 Mar 2003
Start of experiments		
10°C	06 Sep 2002	29 Mar 2003
15°C	27 Aug 2002	31 Mar 2003
18°C	06 Sep 2002	29 Mar 2003
20°C	27 Aug 2002	–
22°C	–	31 Mar 2003

transferred to polyethylene buckets containing 10 l of filtered seawater (< 0.2 µm, salinity 32 psu) with gentle aeration. The eggs were collected from the bottom of the 'parental culture' by sieving through successive nylon screens with 200, 90 and 75 µm meshes in order to exclude adults, copepodites, nauplii and faecal pellets. The fraction collected on the 75 µm sieve was then transferred to a small Petri dish and concentrated to the centre by slow rotating movements and further cleaned by removing early nauplius and detritus. For both populations, each treatment/replicate was set up at the same time. The growth experiments were performed in duplicate at 10, 15 and 18°C with each population. In addition, 1 experiment at 20°C with the northern population and 2 experiments at 22°C with the southern population were performed. All experiments were carried out in a temperature-controlled room, under a 12:12 h light:dark cycle. Food levels were always ≥1000 µg C l^{-1}, which is 3 times higher than the optimal food concentration previously defined for *Acartia clausi* (Klein Breteler & Schogt 1994). The food offered was *Rhodomonas* sp. during naupliar growth (NI to NVI) and a mixture of *Rhodomonas* sp. and *Thalassiosira weissflogii* during the copepodite stages (I to VI). Food concentration was checked daily by an electronic particle counter (Elzone 180XY). Algal biovolume (µm^3) was converted to carbon using the relationship defined by Strathmann (1967). The food concentration was adjusted daily by adding fresh culture and always kept ≥1000 µg C l^{-1}.

Stage duration. The development was followed from Stage NI to the adult stage. Time 0 was defined as the time when eggs were harvested (eggs 0 to 24 h old) and incubation started. Each experiment was sampled daily by mixing the bucket and sieving 100 to 300 ml of water to yield at least 30 individuals for stage determination and length measurements. Total volume of the bucket was kept constant by adding filtered seawater.

The duration of each development stage (stage duration, SD) was calculated as the difference of the median development time (MDT) of 2 successive stages. The MDT of a certain stage was defined as the time when 50% of the organisms in a culture had passed that stage (Landry 1975b, 1983), which in turn was estimated from stage–frequency data converted to stage proportion. The cumulative proportion of each stage over time was plotted against time and a gamma distribution function fitted (Klein Breteler et al. 1994). The relationship between temperature and median development time (from egg to adult) of each population was estimated using Belehradek's function:

$$D = a(T + c)^{-2.05}$$

where D is median development time (days), T is temperature (°C) and a and c are fitted coefficients (McLaren 1995). The coefficients were estimated by non-linear regression using the software Statistica 6.0.

Body-length and weight measurements. Total body length of nauplii (µm) and prosome length of copepodites (µm) were measured with an inverted microscope (100× magnification) with a calibrated eyepiece micrometer. Prosome lengths up to Stage CIII were compared by 2-way ANOVA (population and temperature as factors) and when sexes were discerned (CIV to adults) by 3-way ANOVA (sex, population and temperature as factors). The weight of nauplii (NI to NVI) was estimated from a length–weight regression (Hay et al. 1991). For each copepodite stage at each temperature and population, 10 to 20 individuals were rinsed briefly with distilled water and placed in pre-weighed small aluminium caps. After 24 h at 60°C, the dry weight was measured on a microbalance (Mettler Toledo, sensitivity 1 µg).

Weight-specific growth rates. The body weight of each developmental stage (natural-logarithm transformed) was plotted against cumulative time for each temperature and population, separating nauplii and copepodites. Each data set was then fitted to a linear regression where the slope represents the growth rate (g, d^{-1}). The effects of population (northern and southern), growth phase (nauplii and copepodites) and temperature on growth rate were analyzed through an ANCOVA, where the natural logarithm of dry weight (lnDW) was the dependent variable, development time (days) the covariate and population, growth phase and temperature the independent factors. The relationship between g and temperature was described by a non-linear regression assuming that individuals grow exponentially (Huntley & Lopez 1992, Mauchline 1998).

RESULTS

Stage duration decreased significantly with temperature for both populations (Fig. 1, Table 2). Nearly isochronal growth, with similar stage durations through the late naupliar stages (NIII to NVI) and early copepodite stages (CI to CIII), was noted for both populations (Table 2). The Stage NI was always shorter and Stage NII longer than other naupliar stages. Stage duration tended to increase with age. The estimated generation times equalled 33.9, 20.8 and 16.3 d for the northern population and 36.4, 22.3 and 17.4 d for the southern population at 10, 15 and 18°C, respectively. For each population, the relationship between temperature and generation time was fitted to Belehradek's function (Fig. 2).

The prosome length of all copepodites was longer in the southern population than in the northern population, and prosome length decreased with tempera-

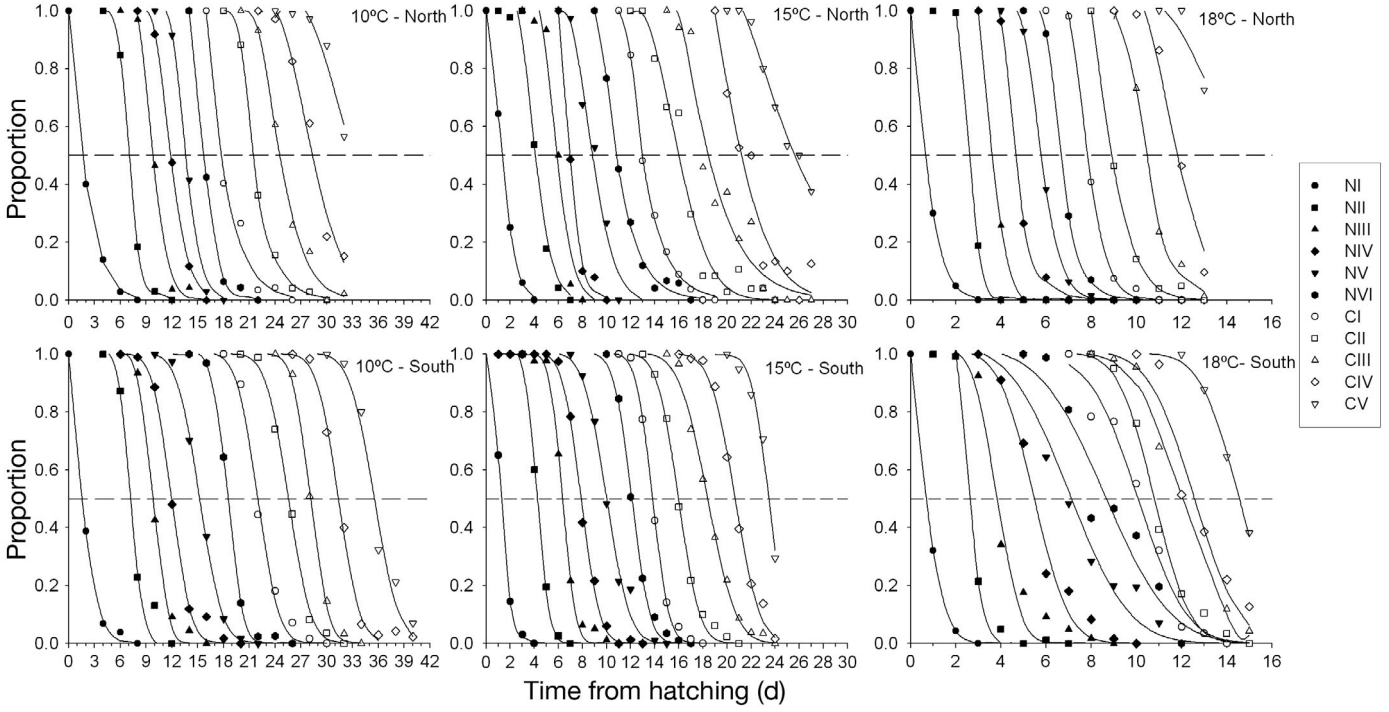

Fig. 1. *Acartia clausi*. Post-embryonic development time for the northern and southern populations reared at 10, 15 and 18°C. For each development stage, a gamma distribution was fitted to the cumulative proportions plotted against time. The intersection between the dashed line (= 50 %) and the fitted Gamma function defines the mean development time (MDT) for the particular stage

ture (Fig. 3). Both effects were significant (2-way ANOVA, $p < 0.001$). The effect of sex (CIV to CVI) was also highly significant (3-way ANOVA, $p < 0.001$), with females always being longer than males. The length ratio of successive stages was nearly constant in both populations, 1.22 (southern) and 1.20 (northern). A length–weight regression for all copepodite stages and adults (both populations pooled) was estimated:

$$\log DW = 2.064 \log PL - 5.080 \quad (r^2 = 0.846, p < 0.001)$$

where DW is dry weight (µg) and PL prosome length (µm).

The weight-specific growth rate (g, d^{-1}) was estimated separately for each temperature and population (Fig. 4) from the slopes of the linear regression of lnDW on cumulative development time. The parameter estimates of the regressions are given in Table 3. An ANCOVA testing for the homogeneity of slopes among the regression lines (Table 4) indicated that for both populations and within a given temperature range, nauplii grew significantly faster than copepodites (ANCOVA homogeneity of slopes, stage × covariate). Exceptions to this rule were noted at 18°C for the southern population and at 20°C for the northern pop-

Table 2. *Acartia clausi*. Stage duration (d) of northern and southern populations estimated at 5 temperatures (°C) and under saturating food conditions (≥1000 µg C l^{-1}). Mean value (± SE), n = 2; where no SE is given, n = 1. Experiments at 20 and 22°C were not performed on both populations

Temp.	NI	NII	NIII	NIV	NV	NVI	CI	CII	CIII	CIV	CV
Northern											
10	2.0 ± 0.39	5.9 ± 0.71	2.6 ± 0.40	2.2 ± 0.12	2.2 ± 0.50	2.4 ± 0.15	2.3 ± 0.39	3.5 ± 0.13	3.3	3.8	4.7
15	1.5 ± 0.20	3.2 ± 0.35	2.0 ± 0.31	1.5 ± 0.40	1.9 ± 0.03	2.3 ± 0.37	2.2	3	2.4	2.8	4.5
18	0.7 ± 0.04	1.9 ± 0.01	1.1 ± 0.17	0.9 ± 0.16	1.2 ± 0.02	0.8 ± 0.05	1.2 ± 0.02	1.1 ± 0.05	1.4 ± 0.06	1.5 ± 0.01	2.8 ± 0.17
20	1.4	2.6	1	0.7	0.7	1	1	0.9	1.6	0.7	1.5
Southern											
10	1.4 ± 0.07	5.4 ± 0.05	2.9 ± 0.15	1.9 ± 0.25	3.4 ± 0.16	3.4 ± 0.04	3.3 ± 0.08	3.9 ± 0.25	2.9 ± 0.25	3.4 ± 0.18	4.4 ± 0.19
15	1.2 ± 0.00	3.0 ± 0.01	2.1 ± 0.02	1.5 ± 0.00	2.1 ± 0.00	2.1 ± 0.00	1.7 ± 0.01	2.2 ± 0.02	2.4 ± 0.01	2.3 ± 0.02	2.9 ± 0.01
18	0.7 ± 0.03	2.1 ± 0.24	1.4 ± 0.23	1.6 ± 0.08	1.4 ± 0.06	1.9 ± 0.17	1.5 ± 0.09	1.0 ± 0.21	1.3 ± 0.19	1.5 ± 1.07	1.4 ± 0.82
22	0.4 ± 0.16	2.1 ± 0.28	1.3 ± 0.28	1.0 ± 0.08	1.2 ± 0.03	1.0 ± 0.04	1.4 ± 0.11	1.0 ± 0.02	1.2 ± 0.05	1.1 ± 0.02	1.9 ± 0.03

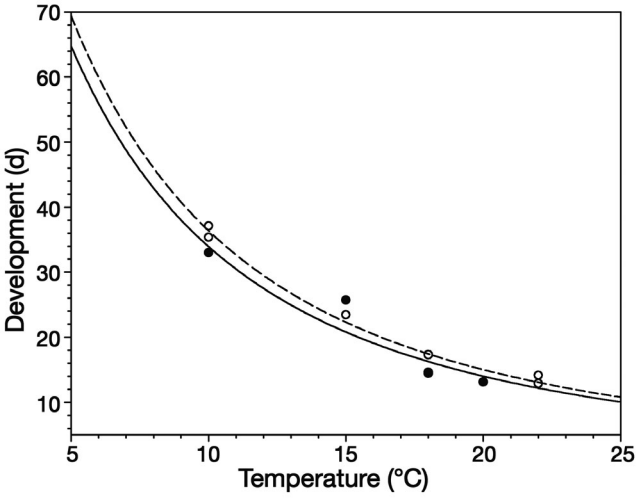

Fig. 2. *Acartia clausi*. Relationship between temperature (T) and generation time (D) for the northern (solid symbols) and southern (open symbols) populations. The estimated parameters of Belehradek's function were: $D = 13490.3(T + 8.53)^{-2.05}$ ($r^2 = 0.897$, $p < 0.01$; solid line) for the northern population, and $D = 14410.4\ (T + 8.50)^{-2.05}$ ($r^2 = 0.978$, $p < 0.001$; dashed line) for the southern population

ulation. Growth rates of nauplii and copepodites of both populations also increased significantly with temperature (ANCOVA homogeneity of slopes, temperature × covariate).

The effect of population was evaluated separately for nauplii and copepodites (within temperature and stage, effect of population). Nauplii from the northern population grew faster than the ones from the southern population, but only at the highest temperature (18°C). No significant differences between the growth rates of copepodites from the northern and southern populations were found. The weight-specific growth rate (g) for both nauplii and copepodites of the *Acartia clausi* populations could be compared using the Huntley & Lopez (1992) equation:

$$g = ae^{(bT)}$$

where T is temperature (°C) and a and b are fitted constants.

The temperature-dependent growth models adjusted for nauplii and copepodites from each population are shown in Fig. 5. The northern population increased growth by 8 to 13% $°C^{-1}$ increase in temperature, whereas the southern population only increased growth by 7 to 8% $°C^{-1}$.

DISCUSSION

The aim of this study was to evaluate the importance of temperature on the development and growth rate of 2 allopatric populations. In the experimental design we therefore kept several other critical parameters constant, such as salinity, food and light:dark cycle. Although the 2 populations can (and probably do) encounter different food conditions in the field, this has been found to affect fecundity of adult females more than somatic growth of other stages (Hirst & Bunker 2003). We cannot exclude that other factors may be more important or that synergistic effects do not exist, but we will only discuss the factor manipulated in the study, temperature.

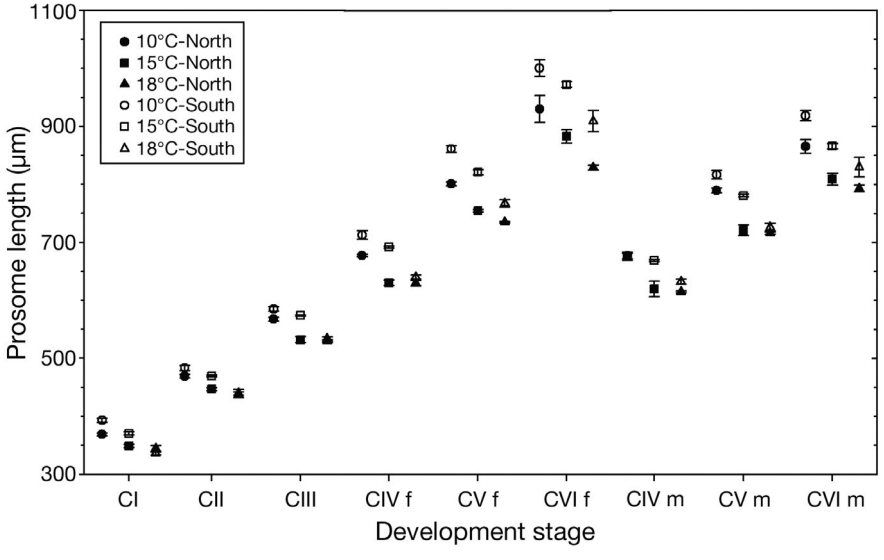

Fig. 3. *Acartia clausi*. Mean prosome lengths of copepodites (CI–CVI, males and females separated from CIV) from the 2 populations. Error bars represent SE

Stage durations

Isochronal development (Miller et al. 1977, Landry 1983) states that, for a given species, the time spent in each developmental stage is the same for all stages (Peterson 2001). We observed a nearly isochronal development of Stages NIII to CIII. A common feature at all temperatures was the relatively short duration of the first naupliar stage. This stage does not feed, but uses lipid reserves to fuel growth. In contrast, 2 stages showed a longer development, NII (first feeding stage) and CV (stage just prior to adult). During Stage NII the animal develops a digestive tract and a foraging behaviour, and a similar prolonged duration has been found in both *Acartia clausi* (Landry

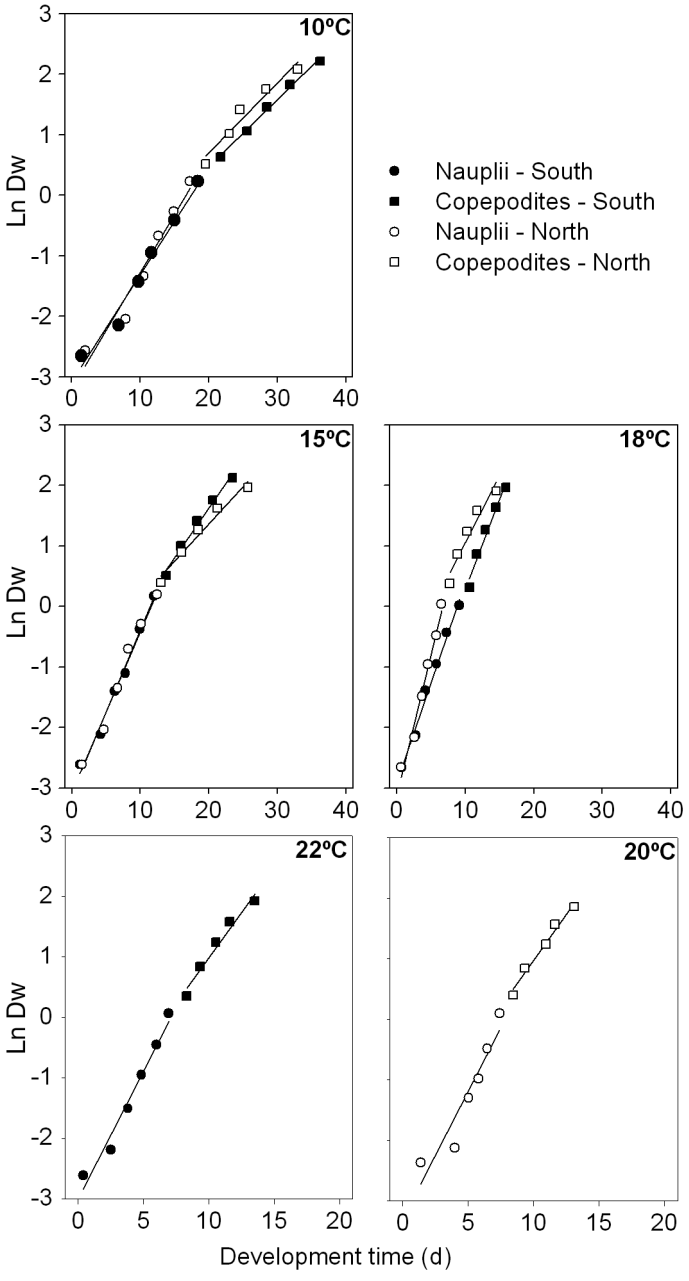

Fig. 4. *Acartia clausi*. Linear regressions of ln-transformed body weight (µg) on cumulative development time (d) for each temperature and population. Nauplii and copepodites are separated and parameter estimates for each regression are given in Table 3

1975b) and *Acartia tonsa* (Berggreen et al. 1988). The increased duration of Stage CV corresponds to the transition to adult males and females during which the animal undergoes external morphological differentiation and sexual maturation (Landry 1983, Peterson 2001). We did not estimate the development time for males and females separately, but it is known that males develop faster than females (Landry 1983). Thus, a significant proportion of duration of Stages CIV and CV is due to to the development of the females. Deviations from the isochronal pattern of development are not limited to *Acartia* spp.; they have been noted in other species, such as *Paracalanus parvus* (Landry 1983), *Pseudocalanus elongatus* (Klein Breteler et al. 1995) and *Calanus finmarchicus* (Campbell et al. 2001).

Development times versus temperature

The 2 allopatric populations of *Acartia clausi* were exposed to different temperature regimes in the field, with the northern population living at lower temperatures, but also experiencing a wider range of temperatures, −1 to 20°C versus 11 to 20°C in the southern population. The northern population had a shorter generation time, even at higher temperatures, than it normally experiences in the field. A strong response to changes in temperature can be selected for if the temperature range experienced by the population is wide. The selection of fast-growing animals in the colder environment could have resulted in different genotypes with specific temperature responses. During juvenile development and growth, the cold-acclimated organisms had a stronger response to temperature than warm-acclimated ones. A similar response to high temperatures has been reported for egg development in *A. clausi* (Landry 1975a,b).

With decreasing temperature, the southern population showed a gradual delay in development compared with the northern population, and the largest difference (2.5 d) occurred at 10°C. This delay could be due to depressed metabolic rates at the lower limit of its thermal range, indicating that the optimum temperature of each population is different. The lower limit of the southern population would occur at higher temperatures than for the northern population.

Body size

Phenotypic plasticity (Atkinson 1994) was exhibited by individuals of both populations when reared at different temperatures. The ontogenetic response to temperature was an increased body length with the decreasing temperature. Increase in size and slow development at low temperatures are common in several marine copepods species. A corresponding shortening of the life cycle at high temperatures would allow a population to take advantage of favourable environmental conditions, by growing faster and achieving maturity earlier (Atkinson 1994). In addition,

Table 3. *Acartia clausi*. Parameter estimates for linear regressions in Fig. 4 and respective significance. Regressions are of the form lnDW = *a* + *bD*, where the slope (*b*) represents the weight-specific growth rate (d^{-1}), DW is the dry weight (µg) and *D* the development time (d) (N – nauplii, C – copepodites)

Temp. (°C)	Population	Stage	*a*	*b*	r^2	p
10	Northern	N	–3.197	0.192	0.958	<0.001
		C	–1.616	0.116	0.949	<0.001
	Southern	N	–3.093	0.177	0.979	<0.001
		C	–1.744	0.111	0.994	<0.01
15	Northern	N	–3.105	0.272	0.984	<0.001
		C	–1.106	0.124	0.971	<0.01
	Southern	N	–3.061	0.265	0.988	<0.001
		C	–1.658	0.164	0.986	<0.001
18	Northern	N	–3.133	0.468	0.981	<0.001
		C	–1.143	0.220	0.935	<0.01
	Southern	N	–2.902	0.330	0.989	<0.001
		C	–2.741	0.301	0.970	<0.01
20	Northern	N	–3.304	0.421	0.891	<0.01
		C	–2.107	0.308	0.977	<0.01
22	Southern	N	–3.009	0.423	0.973	<0.001
		C	–2.024	0.301	0.965	<0.01

Table 4. *Acartia clausi*. Results from ANCOVA comparing *g* (weight-specific growth rate) and the slopes in Fig. 4 and Table 3. Tests are for homogeneity of slopes within growth phase (effect of temperature), within a given temperature (effect of growth phase) and within temperature and stage (effect of population). Growth phase is for nauplii or copepodites

		df	*F*	p	Pairwise comparisons
Within growth phase, effect of temperature					
Northern population	Nauplii	3,16	13.2	<0.001	20°C = 18°C > 15°C > 10°C
	Copepodites	3,12	10.8	<0.001	20°C > 18°C > 15°C = 10°C
Southern population	Nauplii	3,16	29.3	<0.001	22°C > 18°C > 15°C > 10°C
	Copepodites	3,12	28.1	<0.001	22°C = 18°C > 15°C > 10°C
Within temperature, effect of growth phase					
Northern population	10°C	1,7	8.1	0.025	Nauplii > copepodites
	15°C	1,7	47	<0.001	Nauplii > copepodites
	18°C	1,7	27.9	<0.001	Nauplii > copepodites
	20°C	1,7	1.5	0.264	Nauplii = copepodites
Southern population	10°C	1,7	17.6	0.004	Nauplii > copepodites
	15°C	1,7	27.5	<0.001	Nauplii > copepodites
	18°C	1,7	0.7	0.419	Nauplii = copepodites
	22°C	1,7	5.6	0.049	Nauplii > copepodites
Within temperature and stage, effect of population					
Nauplii	10°C	1,8	0.4	0.545	Northern = southern
	15°C	1,8	0.1	0.786	Northern = southern
	18°C	1,8	15.1	0.005	Northern > southern
Copepodites	10°C	1,6	0.1	0.79	Northern = southern
	15°C	1,6	5.8	0.052	Northern = southern
	18°C	1,6	3	0.133	Northern = southern

a physiological explanation for this pattern is that, in the majority of ectotherm species, an increased temperature would increase rates of growth and differentiation and thereby reduce the size at a given stage due to the imbalance between anabolic and catabolic reactions (Ray 1960). This negative correlation of prosome length with temperature has been found in several copepod species both in the field (e.g. Hirst et al. 1999) and in laboratory studies (e.g. Campbell et al. 2001). In addition to phenotypic plasticity, our study also indicated a latitudinal variation in the prosome length of *Acartia clausi*. The copepodites and adult females from the southern population were always significantly larger than the north at a given temperature. This conclusion contradicts the general rule about the influence of temperature on the prosome length of copepods. However, the fact that at a given temperature the southern population had slower development rates than the northern population could justify such latitudinal variation.

Growth rates

At high temperatures, the northern population grew faster than the southern population, and this was due to a faster naupliar development. Growth rates estimated from the general equation of Huntley & Lopez (1992) were always higher than those observed for copepodites (Fig. 5). At 22°C, the Huntley & Lopez model overestimates growth of copepodites of the southern population by 36%. The Huntley & Lopez model is based on estimates for many species with different tolerances inhabiting regions with variable temperature ranges. As we show here, 2 populations of the same species may respond differently when subjected to the same temperature, depending on genetic differences or different temperature history of the individuals. *Acartia clausi* from the southern population may be at the thermal limit for growth at 22°C, whereas the Huntley & Lopez model should fit species at their thermal optimum, since it is based on field measurements.

Populations exposed to extremes of their natural environmental conditions

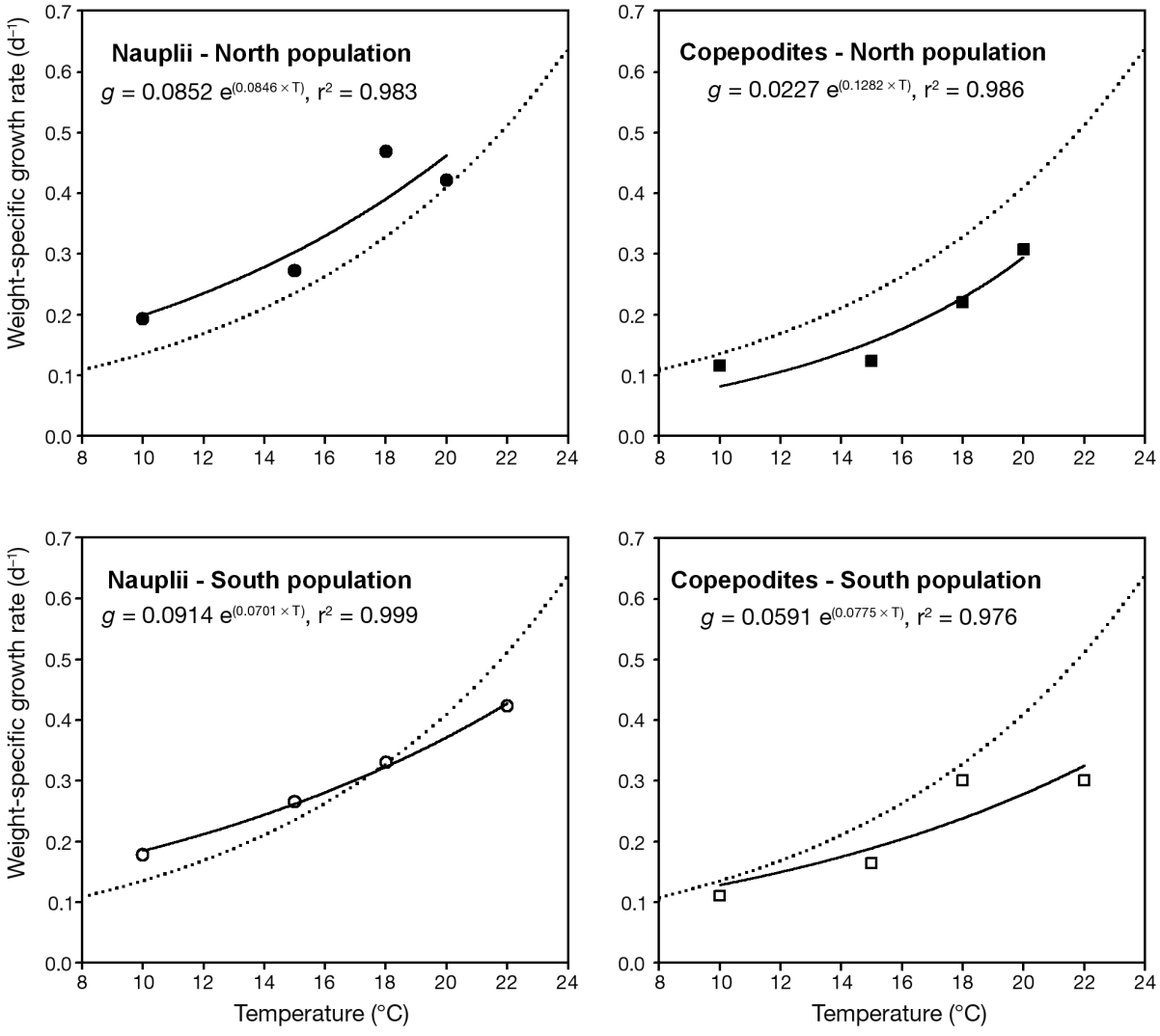

Fig. 5. *Acartia clausi*. Non-linear regression of the weight-specific growth rate (g, d^{-1}) on temperature (T, °C) for nauplii and copepodites of both populations. The relationship proposed by Huntley & Lopez (1992) is indicated by the dashed line

(like our experimental treatments) will not fit the model well. Conversely, population responses to extreme conditions in the field will not be well predicted by the model. We suggest the use of specific growth models instead of general models if estimates of potential growth rates are sought.

In conclusion, this study demonstrates that 2 allopatric populations of *Acartia clausi* exhibit different development rates when reared at the same temperature. It also indicates the existence of differences in growth rates between populations, particularly when reared at high temperatures, with the northern population (acclimated to cold temperatures) growing faster than the southern population (warm acclimated). Finally, the 2 populations showed different ontogenetic responses to temperature shifts. The northern population had a shorter naupliar phase over all temperatures and increased the growth of copepodites at the highest temperature. This suggests that the 2 populations have developed slightly different survival strategies to adapt to their main area of occurrence.

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